

## Influence of within-field and landscape factors on aphid predator populations in wheat

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### Abstract

The influence of prey density, within-field vegetation, and the composition and patchiness of the surrounding landscape on the abundance of insect predators of cereal aphids was studied in wheat fields in eastern South Dakota, USA. Cereal aphids, aphid predators, and within-field vegetation were sampled in 104 fields over a three year period (1988–1990). The composition and patchiness of the landscape surrounding each field were determined from high altitude aerial photographs. Five landscape variables, aggregated at three spatial scales ranging from 2.6 km<sup>2</sup> to 581 km<sup>2</sup>, were measured from aerial photographs. Regression models incorporating within-field and landscape variables accounted for 27–49% of the variance in aphid predator abundance in wheat fields. Aphid predator species richness and species diversity were also related to within-field and landscape variables. Some predators were strongly influenced by variability in the composition and patchiness of the landscape surrounding a field at a particular spatial scale while others responded to variability at all scales. Overall, predator abundance, species richness, and species diversity increased with increasing vegetational diversity in wheat fields and with increasing amounts of non-cultivated lands and increasing patchiness in the surrounding landscape.

### Introduction

The recent widespread trend toward replacement of natural plant communities and diversified agriculture with extensive monocultures has caused a general reduction in faunal diversity, but permitted some phytophagous insects to thrive and become severe pests (van den Bosch and Telford 1973). These changes have affected herbivorous insects directly by altering associations with their host plants, and indirectly through their influence on the natural enemies that normally maintain populations of herbivores below economically important densities (van Emden 1990). Habitat simplification caused by planting monocultures and eliminating weeds can decrease the abundance of natural enemies in agricultural fields and can also decrease the efficiency with which the natural enemies forage for pest insects (van Emden 1990). The structure of the agricultural landscape in which a field is embedded can also influence herbivores and their

natural enemies (Andow 1983; Landis and Marino 1996). Some natural enemies are particularly affected by the loss of non-arable habitats, apparently because of their greater use of alternate resources found in these habitats compared with many herbivorous species (Ryszkowski et al. 1993).

Cereal aphids (Homoptera: Aphididae) thrive in simplified agricultural landscapes and are serious pests of wheat and other small grains (Andow 1983; Way 1988). In the Great Plains of the United States, aphidophagous insects, mostly from the families Nabidae (Hemiptera), Chrysopidae (Neuroptera), and Coccinellidae (Coleoptera), can suppress cereal aphid populations in grain crops (Kring et al. 1985; Rice and Wilde 1988), however control is usually insufficient to curtail economic losses. Plant species diversity in a field can influence the abundance of aphid natural enemies in it (Honek 1986). For example, the presence of weeds in wheat fields is associated with increased abundance of some cereal aphid predators (Sotherton

et al. 1989; van Emden 1990). Plant species diversity is amenable to manipulation by a variety of cultural and chemical treatments applied on an individual field basis. The importance of availability of alternate habitat in the landscape surrounding an agricultural field on the abundance of cereal aphid predators is less well understood than within-field factors, but is believed to play a role in determining the abundance of cereal aphid predators (Honek 1982a; Lattin 1989; Duelli et al. 1990). Increased landscape diversity can influence the abundance of aphid predators in agricultural fields by providing food (e.g., pollen, nectar, and alternate prey), by providing overwintering habitat, or by providing habitat to which the natural enemies can disperse and survive during the period between harvest and emergence of the next crop (Honek 1986).

The composition and grain size of a landscape mosaic can be an important determinant of an organisms population size on both the individual patch and landscape scales; the magnitude of the effect of landscape structure on abundance is directly related to the species ability to disperse (Dunning et al. 1992; Fahrig and Merriam 1994). It follows, that populations of species with different dispersal ability will be affected differently by a change in landscape structure. It also seems reasonable to expect that the effects of variation in landscape structure on a species abundance would be easiest to detect when variation in the landscape is measured at a scale that approximates the area over which an individual disperses during its lifetime.

The tendency for dispersal differs among aphid predator species, and dispersal occurs at different spatial scales and periods during a species life cycle (Duelli 1984; New 1984; Lattin 1989; Hodek et al. 1993). Some aphid predators undergo long-distance flight prior to reaching sexual maturity and before overwintering, but exhibit more restricted flight, mostly related to foraging, during the remainder of their adult life. Other aphid predators apparently never take long-distance flights (Hodek et al. 1993). The characteristics of dispersal related to foraging also differ among species (Ewert and Chaing 1966; Elliott et al. 1998). For example, the coccinellid *Hippodamia convergens* Guerin-Meneville exhibits more frequent flights related to foraging than *Coleomegilla maculata lengi* Timberlake (Ewart and Chaing 1966).

A question of both theoretical and applied interest is, can agricultural landscapes be manipulated to improve biological control of cereal aphids? This study was initiated to address that question. Specifically, we identified characteristics of wheat fields and the land-

scape matrix surrounding them that were important in determining the abundance of cereal aphid predators in the wheat fields. We conducted the study in wheat fields that exhibited a wide range in wheat plant density and growth, weed density, and aphid density. These factors vary from field to field, depending on management practices, and are believed to be important in determining the quality of the field as habitat for aphid predators (Honek 1986). The landscape matrix surrounding the wheat fields also exhibits a wide range of variation in the composition and size of the landscape elements that comprise it. We examined the effects of landscape structure at three spatial scales in an attempt to encompass the characteristic scales over which movement of various predator species takes place. We hypothesized that predator abundance, species richness, and diversity would increase as: (1) aphid density increased; (2) the vegetational diversity in fields increased and the patch size decreased; (3) non-arable and semi-natural lands increased in abundance in the surrounding landscape; and (4) the spatial scale at which landscape structure exerted an influence on a species abundance would depend on the species propensity for dispersal.

## Materials and methods

### *Within-field measurements*

Aphidophagous insects and habitat variables were sampled in wheat fields distributed across six eastern South Dakota counties (Figure 1). Twenty-four to 42 fields were sampled each year from 1988 through 1990. Fields from each county were selected each year for sampling. A particular field was sampled only once during the study. Fields were sampled during June of each year to reduce the effects of seasonal variation on insect and plant populations. Single factor analysis of variance [PROC GLM (SAS Institute 1988)] was used to test for differences among years in the abundance of aphid predator species. Predator abundance data were transformed to natural logarithms prior to conducting analysis of variance because preliminary observation showed that the variance increased with mean abundance (Hoaglin et al. 1983, p. 111).

A single 50 × 100 m study plot was established at a random location in each field (Figure 2). Aphid predators, aphids, and vegetation within the plot were sampled. Aphid predators were sampled by taking six 50-sweep samples with a 38-cm diameter sweep-net (total of 300 sweeps) along approximately equal

*Table 1.* Landscape, habitat, and covariables recorded for each wheat field sampled for aphid predatory insects. Covariables were used as regressors to adjust predator abundance and habitat variables for temporal variability.

Variable	Purpose	( $\bar{x}$ ) range
<b>Habitat variables</b>		
wheat coverage	measure habitat quality for predators	(3.81) 1.7–5.0
broadleaf weed coverage	measure habitat quality for predators	(0.53) 0.0–3.0
grass coverage	measure habitat quality for predators	(0.70) 0.0–3.3
wheat plant height (cm)	measure habitat quality for predators	(58.4) 24–103
aphid density (no./0.09 m <sup>2</sup> )	measure habitat quality for predators	(10.2) 0–283
<b>Landscape variables</b>		
Fine scale (1.6 × 1.6 km)		
% grassland & pasture	measure landscape composition	(14.2) 0.5–45.7
% woods	measure landscape composition	(3.3) 0.0–35.9
% CRP	measure landscape composition	(4.2) 0.0–38.5
% wetlands & water	measure landscape composition	(4.3) 0.0–61.9
no. boundaries crossed	measure landscape patchiness	(13.8) 2.0–37.0
Intermediate scale (4.8 × 4.8 km)		
% grassland & pasture	measure landscape composition	(17.7) 4.4–57.5
% woods	measure landscape composition	(3.4) 0.0–42.2
% CRP	measure landscape composition	(5.4) 1.0–12.6
% wetlands & water	measure landscape composition	(4.9) 0.0–47.0
ave. no. boundaries crossed	measure landscape patchiness	(14.0) 6.2–24.8
Broad scale (24.1 × 24.1 km)		
% grassland & pasture	measure landscape composition	(17.3) 7.3–32.1
% woods	measure landscape composition	(3.0) 2.0–5.8
% CRP land	measure landscape composition	(5.2) 0.0–16.2
% wetlands & water	measure landscape composition	(4.3) 0.7–15.7
ave. no. boundaries crossed	measure landscape patchiness	(13.8) 9.4–16.0
<b>Covariables</b>		
year	adjust habitat and predator variables	(1989) 1988–1990
day of the year	adjust habitat and predator variables	(170.5) 156–181
wheat growth stage (1–10 scale)	adjust habitat and predator variables	(5.1) 3.0–7.1
time of day (h)	adjust predator variables	(1434) 1100–1700
windspeed (m/s)	adjust predator variables	(3.25) 0.08–10.0
air temperature (°C)	adjust predator variables	(25.8) 15.6–37.8
relative humidity (%)	adjust predator variables	(55.0) 33–79
solar radiation (w/m <sup>2</sup> )	adjust predator variables	(1109) 325–1600

spaced transects through the plot. The number of each aphid predator species in each 50 sweep sample was recorded. Ambient air temperature (°C), percent relative humidity, solar irradiance (w/m<sup>2</sup>), and windspeed (m/s) were measured just prior to, and just after sweepnet sampling because these meteorological variables are known to influence the efficiency of sweepnet sampling in wheat fields for some aphid predators (Elliott et al. 1990; Michels et al. 1997).

Habitat variables were measured within each plot using a systematic sampling method in which 15 sam-

ples were taken at approximately equidistant locations in the plot (Figure 2). The following habitat variables were measured at each location: wheat plant height (cm); wheat plant growth stage (Zadoks et al. 1974); canopy coverage by wheat, herbaceous plants, and grasses; the number of wheat tillers (stems) per 0.3-m of crop row; the distance between planted rows; and the number of aphids per tiller. The canopy coverage sampling method involves scoring, on a scale of 0 to 5, the area of a 20 × 50 cm quadrat encompassed by the canopy of each plant group being sampled (Dauben-

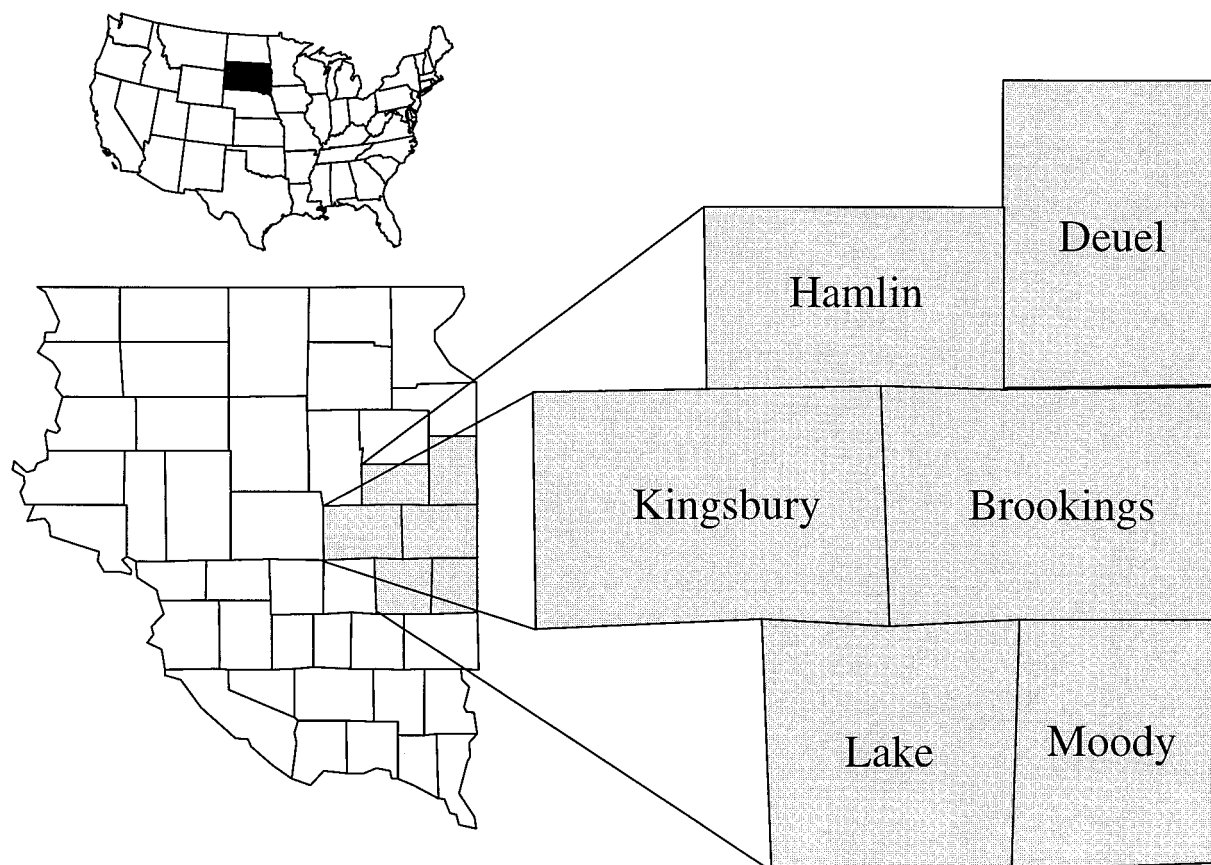


Figure 1. The six county study area in eastern South Dakota.

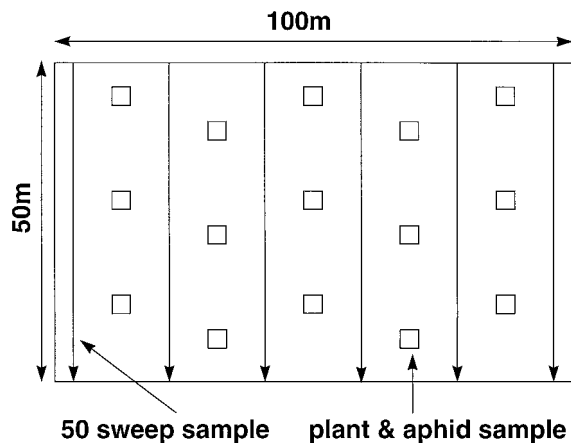


Figure 2. A schematic diagram of a study plot in a wheat field.

mire 1959). A score of 0 indicates that the canopy of a particular plant type covers 0–5% of the area of the quadrat, whereas a score of 5 indicates greater than 95% coverage. Cereal aphids were sampled at each

of the 15 locations by selecting a single wheat tiller at each of three arbitrary locations within arm's reach of the observer and counting the number of aphids on each tiller.

During 1989 and 1990 we measured abundances of small (<1 cm) and large (>1 cm) insect larvae (mostly Lepidoptera) and plant bug (Hemiptera, Miridae) nymphs and adults in wheat fields. Abundances of these potential prey for aphid predators were expressed as the average number in each category per 50 sweeps, for the six 50-sweep samples used to measure aphid predator abundance in wheat fields. Because data on these potential alternate prey were limited to only two of the three years, they were not used as independent variables in regressions relating predator abundance to within-field and landscape factors (described below).

Table 2. Abundance of aphid predators (number caught per 50 sweeps), species richness, and Shannon–Weiner diversity in 300 sweep samples from wheat fields in eastern South Dakota during 1988–1990. The number of fields sampled each year are in parentheses.

Species	$\bar{x}(SE)$		
	1988 (24)	1989 (38)	1990 (42)
<i>Nabis americanoferus</i> *	5.36 (1.80)	1.11 (0.21)	5.01 (0.69)
<i>Chrysoperla plorabunda</i> *	0.37 (0.07)	0.50 (0.12)	2.84 (0.45)
<i>Hippodamia convergens</i> *	5.24 (1.71)	2.67 (0.77)	0.22 (0.07)
<i>Hippodamia parenthesis</i> *	1.65 (0.94)	0.20 (0.07)	0.24 (0.05)
<i>Coleomegilla maculata</i> *	0.45 (0.10)	0.22 (0.06)	0.28 (0.07)
<i>Coccinella septempunctata</i>	0.44 (0.13)	0.94 (0.37)	0.97 (0.27)
Other species*	0.72 (0.37)	0.04 (0.01)	0.16 (0.05)
Total predator abundance*	14.23 (3.95)	5.68 (1.22)	9.72 (1.20)
Species richness*	5.42 (0.53)	3.46 (0.26)	4.09 (0.28)
Shannon–Weiner diversity*	1.03 (0.11)	0.90 (0.07)	0.89 (0.04)

\*Means within a row differ significantly ( $P < 0.05$ ).

### Landscape measurements

The composition and heterogeneity of the landscape surrounding each field was determined from high altitude aerial panchromatic photographs obtained from the U.S. Agricultural Stabilization and Conservation Service (now The U.S. Farm Service Agency). Land use was grouped into four classes: grassland/pasture, wooded, USDA Conservation Reserve Program (CRP) lands, and wetlands/water. Land enrolled in the CRP is planted to grasses, but is not grazed, mowed, or burned. The remainder of the land in each section was mostly cultivated fields, but some land was covered by man-made structures such as farmsteads and roads; area of land in these categories was not recorded. The number of hectares in each of the four land use categories was calculated for each of nine  $1.6 \times 1.6$  km blocks centered on the block containing the sampled field (Figure 3). These data were then expressed as the percentage of the total area of each block covered by each land use type. The density of boundaries between land use types was estimated for each block by drawing two straight lines from corner-to-corner across the diagonals of the block and counting the number of boundaries crossed between land use types along the length of each line. We treated boundary density as a measure of the grain size of the landscape, hereafter referred to simply as ‘patchiness’.

Landscape data were aggregated at three spatial scales (Figure 3). At the finest scale, land use and patchiness surrounding a study field in a particular  $1.6 \times 1.6$  km block were represented by the data for

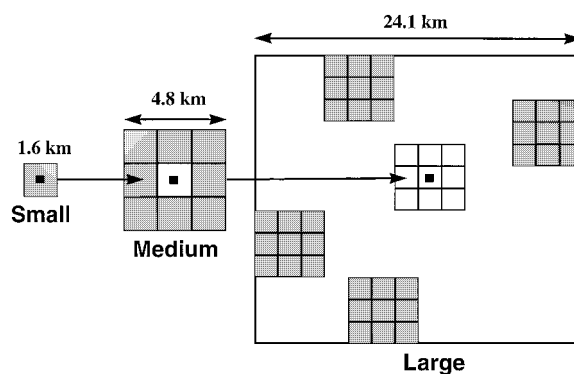


Figure 3. The three spatial scales over which landscape data were aggregated.

that particular block. At the intermediate scale, the data for the eight  $1.6 \times 1.6$  km blocks immediately adjacent to the block containing the sampled field, but excluding data for the block containing the field, were averaged. At the broadest scale, data for 9 contiguous  $1.6 \times 1.6$  km blocks within a  $24.1 \times 24.1$  km block centered on the block containing the sampled field were averaged. In this case, data for the nine blocks containing the sampled field were excluded. Measurement of landscape variables for  $24.1 \text{ km}^2$  blocks was not exhaustive. The number of nine block units within the  $24.1 \text{ km}^2$  block for which landscape variables were measured varied from 5 to 8. Aggregating the data at multiple scales provided a means for assessing the approximate scale at which landscape influences on aphid predator populations were greatest and could best be detected.

### Stepwise multiple regression models

In total there were five variables describing the habitat within a field and 15 (5 landscape variables  $\times$  3 spatial scales) landscape variables. Since we were interested in the influence of variability within a field and within a landscape on the abundance, species richness, and Shannon–Weiner diversity of aphidophagous insects in wheat fields rather than on the influence temporal variability, variables such as air temperature and wheat plant growth stage were used as covariables in regressions to adjust response variables, such as predator abundance, and independent variables, such as canopy coverage by broadleaf weeds, prior to subjecting these variables to stepwise multiple regression modeling. All variables and their purpose are summarized in Table 1.

Many of the landscape variables were correlated so principal components analysis [PROC Factor (SAS Institute 1988)] was used to reduce the number of variables in the data set and to clarify their interpretation. The number of principal components retained for use as regressors in linear regressions was determined by the scree method. The scree method involves plotting the eigenvalue associated with each principal component in successive order of extraction and determining the point beyond which the smaller eigenvalues form an approximately straight line. The components retained are those associated with eigenvalues that fall above the straight line formed by the smaller eigenvalues (Dillon and Goldstein 1984, p. 47–50).

The effects of within-field and landscape factors on predator abundance, species richness, and Shannon–Weiner diversity could be difficult to identify by stepwise regression modeling if variables measured at the two scales were correlated (Pearson 1993; Pedlar et al. 1997). When a variable from one spatial scale is included in the model, a variable from the other scale with which it is correlated may be overlooked because much of its influence on the dependent variable is accounted for by inclusion of the first variable. There was little reason to suspect that within-habitat variables would be correlated with landscape variables in our data because most within-habitat variables were determined primarily by farm management practices, such as planting date and herbicide use, which should have little relationship to the surrounding landscape. Preliminary analysis showed that seven of a possible 75 correlation coefficients between habitat and landscape variables were significant at the  $\alpha = 0.05$  level, only slightly more than would be expected by chance.

Furthermore, none of the correlation coefficients was greater than 0.27 in absolute value. Based on that evidence, we concluded that confounding of the effects of within-field and landscape factors in multiple stepwise regression models would be minimal.

Multiple regression models were developed using PROC REG (SAS Institute 1988). Response variables included the abundance of each predator species (number caught per 50 sweeps), species richness, and Shannon–Weiner diversity (Shannon and Weaver 1948). Prior to including within-field and landscape factors as independent variables in a stepwise multiple regression model, the response variable was adjusted for temporal variation by regressing it against the covariables listed in Table 1. If visual examination of residuals of first-order regression models indicated non-linear response to variation in one or more covariables, second order, and if necessary, higher order terms were added to the regression model until visual evidence of lack-of-fit disappeared. After species abundance, richness, and diversity data were adjusted for temporal variation, habitat and landscape variables were entered into stepwise multiple regression models. F-tests were used to determine the significance of regression models. The  $\alpha$ -value for inclusion of an independent variable in a regression model was 0.05 unless otherwise stated in the results.

## Results

### General patterns

Nine aphidophagous insect species were captured in wheat fields in eastern South Dakota during this study (Table 2). The common damsel bug, *Nabis americanoferus* Carayon (Hemiptera: Nabidae), was the most abundant aphid predator, followed by the convergent lady beetle, *Hippodamia convergens*. Less abundant predators included the common green lacewing, *Chrysoperla plorabunda* (Fitch) (Neuroptera: Chrysopidae), and the coccinellids, *H. parenthesis* (Say), *Coleomegilla maculata lengi*, *Coccinella septempunctata* (L.), *H. tredecimpunctata tibialis* (Say), *Coccinella transversoguttata richardsoni* Brown, and *Cycloneda munda* (Say). Three species, *H. tredecimpunctata tibialis*, *C. transversoguttata richardsoni*, and *C. munda*, were encountered too infrequently to permit construction of regression models to describe their abundance in wheat fields.

The abundance of most aphid predators differed among years of the study (Table 2). The abundance

Table 3. Interpretation of landscape principal components after varimax rotation. The factors summarize variation in 5 variables representing the abundance of 4 semi-natural habitat types and the patchiness of the landscape surrounding each sampled field at three spatial scales.

Principal component name	Description	% total variance
L1	CRP and woods at all scales	0.17
L2	All non-arable habitats except wetlands, and landscape patchiness at broad scale	0.14
L3	Wetlands at fine and intermediate scales	0.13
L4	Pasture and woods, and landscape patchiness at intermediate scale	0.13
L5	Pasture and landscape patchiness at fine scale	0.11
L6	CRP and woods at fine scale	0.11
L7	Wetlands at broad scale	0.07
% total variance explained		86.0

Table 4. Stepwise multiple regression models for aphid predator abundance and species diversity. Variables are listed in decreasing order of their contribution to model  $R^2$ . Model  $R^2$  gives the individual contribution of each variable after accounting for previously entered variables, including covariables. The contribution of covariables to total  $R^2$  is listed separately.

Name	Variables included	$R^2$ -model	$R^2$ -covariables
<i>Nabis americanoferus</i>	$0.72 \times L1 + 0.69 \times L4 + 0.16 \times \text{aphid density}^*$	0.12, 0.09, 0.06	0.24
<i>Chrysoperla plorabunda</i>	$0.41 \times L4 + 0.14 \times \text{aphid density}$	0.16, 0.11	0.48
<i>Hippodamia convergens</i>	$2.91 \times \text{crop density} + 3.13 \times \text{broadleaf density} + 0.80 \times L4^*$	0.23, 0.19, 0.07	0.31
<i>Hippodamia parenthesis</i>	$0.39 \times L6^*$	0.10	0.23
<i>Coleomegilla maculata</i>	$0.16 \times L5 + 0.24 \times L6$	0.29, 0.16	0.34
<i>Coccinella septempunctata</i>	$0.59 \times L1 - 0.45 \times L4$	0.14, 0.12	0.24
Total predator abundance	$2.98 \times \text{crop density} + 1.54 \times L1$	0.18, 0.10	0.21
Species richness	$0.39 \times L5 + 0.76 \times \text{broadleaf density} + 0.41 \times \text{crop density}^*$	0.12, 0.07, 0.06	0.20
Shannon–Weiner diversity	$0.07 \times L5 + 0.07 \times L4 + 0.09 \times \text{broadleaf density}$	0.11, 0.10, 0.10	0.19

\*Significant at  $\alpha = 0.10$ .

of most species was greatest in 1988 and lowest in 1989. *Coccinella septempunctata* and *C. plorabunda* did not follow that trend and were least abundant in 1988 and most abundant in 1990. However, the abundance of *C. septempunctata* did not differ significantly among years. Species abundances were often correlated with covariables such as time of day and ambient air temperature at the time of sampling. Regressions against these covariables accounted for 24 to 48% of the variation in abundance of individual species (Table 4). Regressions on covariables accounted for smaller percentages of variation in species richness and Shannon–Weiner diversity than they did for the abundance of individual species (Table 4).

Habitat variables describing the vegetation and prey in wheat fields varied markedly among fields (Table 1). For example, canopy coverage by grasses

ranged from 0 to 3.3, while canopy coverage by wheat ranged from 1.7 to 5.0. Habitat variables (Table 1) fluctuated temporally and were regressed against year, day of the year, and crop growth stage. The residuals of these regressions were used as independent variables in the stepwise phase for variable inclusion in the multiple regression models for species abundance and diversity.

Aphid abundance was generally low in fields, ranging from 0 to 283 aphids per 0.09 m<sup>2</sup>. Four species of cereal aphids occurred in wheat fields each year: *Rhopalosiphum padi* (L.), *R. maidis* (Fitch), *Schizaphis graminum* (Rondani), and *Sitobion avenae* (Fabricius). Aphids were not identified to species during sampling, but field notes indicate that *R. padi* was the most abundant species in 1989 and 1990, while *S. graminum* predominated in 1988. Species other than

the dominant one in a particular year were present in low numbers in most fields.

Landscape variables also varied widely (Table 1). For example, the percentage of CRP land at the finest scale ranged from 0 to 38.5% of all land in the 1.6 km<sup>2</sup> block containing the sampled field, while the average number of boundaries crossed ranged from 2.0 to 37.0 ( $\bar{x} = 6.9$ ).

#### *Principal components analysis of landscape variables*

Examination of a scree plot of the principal component eigenvalues showed that the first seven components were adequate to describe variation in the 15 original landscape variables and accounted for 86% of the variation in the original data. These seven components were rotated by varimax rotation (Dillon and Goldstein 1984, p. 91–92). The rotated principal components were interpreted based on magnitudes of component loadings on the original variables (see Appendix 1) and are described in Table 3. Some components reflected variation in landscape composition and patchiness at a particular spatial scale. For example, component L2 had large positive loadings for most land use classes and for patchiness at the broadest spatial scale, but very small loadings that varied in sign for these same classes and for patchiness at the intermediate and fine scales. Component L4 describes variation in the percentage of the landscape in pasture and woods, and landscape patchiness at the intermediate spatial scale. Components L5 and L6 represent variation in landscape composition and patchiness at the finest spatial scale. Component L1 represents the proportion of land in CRP and woods at all spatial scales. This component reflects the fact that CRP lands were often associated with woods. This probably results from a tendency for farmers to enroll poor agricultural fields in topographically diverse terrain, which also tend to be more heavily wooded, in the CRP.

#### *Effects of within-field and landscape factors*

Temporal variation in aphid predator populations was removed by regressing abundance for each species against covariables listed in Table 1 prior to introducing habitat and landscape variables in the stepwise phase of multiple regression modeling. The percentage of variation in abundance accounted for by all covariables ranged from 19 to 48% (Table 4). Covariables generally accounted for nearly as much of

the variation in abundance as landscape and within-field variables combined. When the influence of these factors was removed from the data, we were able to distinguish effects of variation in landscape structure, within-field vegetation, and aphid abundance on aphid predator abundance.

Both landscape and within-field variables influenced the abundance and species diversity of aphid predators in wheat fields (Table 4). However, landscape variables were included in regression models more frequently than within-field variables, and for five of six species, accounted for a greater percentage of variation in abundance (Table 4). Aphid density was a significant variable in the regression for the abundance of only one species, *C. plorabunda*; it was significant at the  $\alpha = 0.10$  level for *N. americanoferus*.

Abundances of the six common predator species were influenced by landscape variables, as were total predator abundance, species richness, and species diversity (Table 4). Abundance of *C. maculata* was strongly influenced by landscape composition and patchiness at the finest spatial scale investigated (variables L5 and L6). Variables representing landscape composition and patchiness at broader scales explained very little of the variation in abundance of *C. maculata* (result not shown). Thus, the structure of the landscape in the immediate vicinity of a wheat field had a greater affect on the abundance of *C. maculata* than that farther from it. The abundance of *H. parenthesis* also appeared to be related to the presence of CRP and woods at the finest spatial scale (L6). However, the regression was not significant at the  $\alpha = 0.05$  level, and L6 accounted for only 10% of the variability in abundance. The abundance of *H. convergens* was more strongly related to crop and broadleaf weed density than to landscape factors, but was also related to landscape composition and patchiness at the intermediate scale (L4).

Abundances of *N. americanoferus* and *C. septempunctata* were influenced by the amount of woods and CRP (L1) and by pasture, woods, and landscape patchiness at the intermediate scale (L4). Among landscape factors, variation occurring at the intermediate spatial scale (L4) most strongly influenced the abundance of *C. plorabunda* and *H. convergens*. Overall, landscape composition and patchiness at the fine and intermediate scales were most frequently included in stepwise multiple regressions for predator abundance.

Total predator abundance was related to crop density and L1. This is primarily a reflection of the fact that *N. americanoferus* and *H. convergens*, the two most



abundant aphid predators in wheat fields were most strongly influenced by these two variables. Species richness and diversity were most strongly influenced by the amount of pasture and landscape patchiness at the fine scale (L5) and by the density of broadleaf weeds in wheat fields. A regression for the combined abundance of the three uncommon predator species, *H. tredecimpunctata tibialis*, *C. transversoguttata richardsoni*, and *C. munda* was not significant, but the density of broadleaf weeds was the most influential variable in that regression accounting for 14% of the variance in abundance of these species (result not shown).

## Discussion

The covariables measured in this study explained a large percentage of the variation in aphid predator abundance. This was not surprising because the efficiency of sweepnet sampling for some aphid predators is influenced by meteorological variables, time of day, and the density and growth stage of the wheat crop (Elliott et al. 1990; Michels et al. 1997). The large proportion of total variation accounted for by the covariables illustrates the importance of concomitant environmental measurements in studies of insect populations when relative sampling methods are used. The effects of habitat and landscape factors would have been very difficult to identify if it had not been possible to adjust predator abundance measurements for variation in meteorological and other environmental factors that affected the efficiency of population sampling methods.

The relatively low percentage of the total variation in predator abundance and species diversity accounted for in multiple regression models by habitat and landscape factors (10 to 49%) should not be interpreted as evidence of their limited importance; it is more likely a reflection of the large sampling error associated with our methods, particularly those used to estimate aphid predator abundance. Extensive sampling methods were dictated by logistical constraints resulting from our desire to sample as many sites as possible each year and yet accomplish the sampling in a short time period in order to minimize the effects of seasonal variation on aphid and predator populations in fields, which if not controlled, could have resulted in temporal pseudoreplication (Hurlbert 1984). From a practical standpoint, there is always a trade-off between sampling intensity and the number of samples

that can be obtained. We chose to sample as many fields as possible each year in order to maximize the number of sites available for analysis; but this was accomplished at the expense of precision of estimates of variables for any particular field. As a consequence of our choice, the coefficients of determination of regressions would be expected to be low, as they were, but important variables would still enter into multiple regressions because of the large number of degrees of freedom.

## Aphid predators and within-field factors

Our primary interest was in the effects of factors that might be amenable to management, such as within-field plant species composition, on the abundance of cereal aphid natural enemies. However, prey availability is of obvious importance for aphid predator survival and reproduction and was also investigated.

With the exception of *C. maculata*, which feeds on a variety of arthropods and plant pollen in addition to aphids (Hodek and Honek 1996, p. 149), the coccinellids encountered in wheat fields in eastern South Dakota feed primarily on aphids (Hodek and Honek 1996, p. 169–176). It is well known that adult aphidophagous coccinellids aggregate in fields with high aphid density (Frazer and Gilbert 1976; Evans and Youssef 1992). Therefore, cereal aphid density should have been important in determining the abundance of most coccinellid species in wheat fields. The finding that aphid density was unimportant in regression models for coccinellid abundance was unexpected. The absence of a numerical response by coccinellids to variation in aphid density among fields may reflect the generally low aphid densities encountered in wheat fields during our study. Aphid populations may have been too low to cause the reduction in emigration rate from fields that results in aggregation by coccinellids in them (Hodek and Honek, p. 228).

Aphid density was an important explanatory variable for *N. americanoferus* and *C. plorabunda*. *Nabis americanoferus* and *C. plorabunda* feed on a variety of small, soft-bodied arthropods in addition to aphids (Principi and Canard 1984; Lattin 1989). Evans and Youssef (1992) found that nabid abundance in alfalfa fields was uncorrelated with aphid density and alfalfa weevil (Coleoptera) larval density and suggested that the broad diet of nabids compared to coccinellids may inhibit their numerical response to spatial variation in the density of a particular prey type. In our study, the abundance of *N. americanoferus* increased in

wheat fields with increasing aphid density, suggesting that *N. americoferus* aggregated in fields with high aphid density. It is possible that *N. americoferus* adults were responding to another prey type, the abundance of which was correlated with aphid abundance. The abundance of small (<1 cm) soft-bodied insect larvae, which was measured in 1989 and 1990 but not in 1988, was correlated with aphid abundance ( $r = 0.19$ ;  $P = 0.05$ ). Furthermore, *N. americoferus* abundance was more strongly correlated with the abundance of small larvae ( $r = 0.49$ ;  $P < 0.0001$ ) in fields than it was with cereal aphid abundance ( $r = 0.28$ ;  $P < 0.003$ ). This suggests that aggregation by *N. americoferus* in fields with high aphid density may have been an artifact of the correlation of cereal aphid density with that of other prey. Our results indicate that *N. americoferus* exhibits a numerical response to prey density, whether it be cereal aphids, small insect larvae, or the combined density of several prey types.

*Chrysoperla plorabunda* adults are not predaceous, but feed on aphid honeydew; larvae feed on a broad range of small, soft-bodied arthropods in addition to aphids (Principi and Canard 1984). Appetitive flight by adult *C. plorabunda* terminates when an individual contacts the scent plume of a food source, which causes adults to aggregate in fields with high prey density, where they feed and oviposit (Duelli 1984). The finding that aphid density was an explanatory variable in the regression model for *C. plorabunda* may be viewed with the same suspicion as for *N. americoferus* because *C. plorabunda* abundance was correlated with the abundance of small larvae ( $r = 0.60$ ;  $P < 0.0001$ ) and cereal aphids ( $r = 0.42$ ;  $P < 0.0001$ ). Thus, the numerical response by *C. plorabunda* may have been in response to the density of arthropods other than cereal aphids, or to their combined density. The fact that the coccinellids encountered in wheat fields in eastern South Dakota feed primarily on aphids, yet showed no numerical response, whereas *N. americoferus* and *C. plorabunda* feed on a broad range of soft-bodied arthropods in addition to aphids increases our suspicion that aggregation by the latter two species in fields may have been at least partially in response to the density of non-aphid prey.

Plant community composition and physical structure (probably partly due to their influence on microclimate) are important in determining aphid predator abundance and distribution in corn fields in North America (Smith 1971; Coderre et al. 1987) and wheat fields in central Europe (Honek 1982, 1983). Honek

(1982, 1983) found that coccinellids were sensitive to wheat plant density; adults of some species prefer dense stands, while others prefer sparse stands. The abundance of *H. convergens* increased with increasing crop and broadleaf weed density indicating that this species prefers dense stands. Thus, a response by coccinellids to vegetation density, similar to that observed by Honek (1982, 1983), occurs for at least one species in eastern South Dakota. Species richness was also influenced by broadleaf weed density suggesting that the presence of weeds in wheat fields was particularly important in determining the abundance of the uncommon coccinellids encountered in this study, *H. tredecimpunctata tibialis*, *C. transversoguttata richardsoni*, and *C. munda*.

#### *Aphid predators and landscape factors*

Landscape variables were generally more influential than within-field variables for explaining variation in aphid predator abundance, species richness, and Shannon–Weiner species diversity. However, sampling error associated with measurements of landscape and habitat variables differed depending on the particular variable, making it impossible to assess the relative importance of a variable based solely on the amount of variation in predator abundance accounted for by it in a regression model. For example, measurements of habitat variables were made by sampling plant populations using established methods, but these measurements were subject to sampling error. Conversely, landscape variables at the fine and intermediate scales were measured for the entire land area surrounding a field and were not subject to sampling error. This may have rendered the effects of within-habitat factors less evident causing their importance to be underestimated. This limitation notwithstanding, it is notable that landscape variables were included in all multiple regressions indicating their widespread importance as determinants of aphid predator abundance and species diversity in wheat fields in eastern South Dakota.

The aphid predators we encountered possess the capacity for long-distance dispersal. Whether or not such dispersal occurs, and how frequently and under what conditions it occurs, is not well documented for most species. Dispersal characteristics undoubtedly differ among species (Hodek et al. 1993; Hodek and Honek 1996; Duelli 1984). Landscape influences on aphid predator abundance and species diversity in wheat fields probably reflect the relationship between

a species propensity to disperse and landscape structure. The structure of the landscape surrounding a wheat field could affect predator populations in the field in several ways, two of which may be particularly important. First, the availability of a diversity of habitats in a fine grained landscape mosaic could increase aphid predator numbers during the growing season by providing prey nearby at times when it is scarce or absent in wheat fields, thus increasing predator survival and reproduction and retaining predators in the vicinity of the field (Honek 1982a; Duelli 1988; Hemptinne 1988). Second, semi-natural lands could provide acceptable overwintering habitat near cultivated fields so that predators could colonize the fields earlier and in greater numbers the following spring (Honek 1982a, Hemptinne 1988).

From our results it is not possible to determine whether the availability of alternate prey or of overwintering sites accounted for the effects of landscape factors on these aphid predators. However, interpretation of regression models in light of species life histories may yield insight. The regression model for *C. maculata* demonstrates a particularly strong influence of the surrounding landscape on its abundance in wheat fields. This species is capable of long-distance flight (Solbreck 1974), but during the growing season it appears to be relatively sedentary when compared to *H. convergens* and *H. tredecimpunctata tibialis* (Ewert and Chiang 1966). *Coleomegilla maculata* is probably also more sedentary than *C. septempunctata* (Honek 1982b, 1990) and *C. plorabunda* (Duelli 1984, 1988), although direct comparisons with these two species have not been made. It is polyphagous and can complete its life cycle on pollen from a number of plants, although its development time is increased and fecundity decreased compared to when feeding on aphids and pollen (Smith 1965). Some aphid predators undergo directional flights over very long-distances to overwintering habitats in autumn (Hodek et al. 1993). However, *C. maculata* overwinters primarily in leaf litter along woodland edges and hedgerows in the general vicinity of its feeding and breeding habitats (Solbreck 1974; Roach and Thomas 1991). The broader diet and absence of long-distance flights between breeding and overwintering sites may explain the reduced movement of *C. maculata* compared with the more oligophagous coccinellid species. Thus, compared with many aphid predators, the population dynamics of *C. maculata* in a particular field may be expected to be more closely related to features of the landscape in the immediate vicinity of the field. The

inclusion of woods and patchiness at the fine spatial scale in the regression model might have been anticipated based on knowledge of its life history.

In a multi-year comparison of numbers of dispersing coccinellids caught on sticky traps with their abundance in adjacent agricultural fields in eastern South Dakota, *H. parenthesis* was caught in lower numbers compared to its abundance in fields than most other species (Kieckhefer et al. 1992; Elliott et al. 1998), suggesting that this species may also be relatively sedentary. Thus, *H. parenthesis* might also be expected to respond to landscape variability on a relatively fine spatial scale. Because of the high mobility of *C. plorabunda* (Duelli 1984), *C. septempunctata* (Honek 1982b), and especially *H. convergens* relative to *C. maculata* and *H. parenthesis*, inclusion of landscape variables at broader scales seems intuitively reasonable.

The inclusion of landscape factors in the model for *N. americoferus* abundance is difficult to explain because very little is known about its dispersal characteristics or patterns of habitat use in agricultural landscapes. *Nabis americoferus* is capable of flight and is frequently caught in flight interception traps stationed near agricultural fields (McPherson and Weber 1981; R. W. Kieckhefer unpublished). This predator commonly overwinters within agricultural fields or in field margins, thus using essentially the same habitats for feeding, breeding, and overwintering. Furthermore, it feeds on a broader range of arthropod prey than coccinellids (Lattin 1989). These observations suggest that *N. americoferus* should be less dependent on landscape composition than most aphid predators we encountered, and that it would prosper in the ephemeral habitats that typically dominate agricultural landscapes. Our results suggest, however, that this species responds to landscape heterogeneity in a manner qualitatively similar to the more oligophagous aphid predators we encountered.

Landscape variability at the broadest spatial scale we investigated was incorporated in regression models for predator abundance through inclusion of the variable L1, which describes variation in landscape composition at all spatial scales. However, if broad scale landscape characteristics were important in determining the abundance of an aphid predator species, we would expect that L2, which describes variation in the amount of semi-natural land and landscape patchiness at the broad scale, would have been a significant variable in a regression model for that species. The fact that L2 was never included in regression

models for predator abundance, or for species richness or Shannon–Weiner diversity leads us to suggest that the broad spatial scale was larger than the area over which ecologically relevant movement of these predators occurs.

### *Land use patterns and biological control*

The spatial extent of influence of the landscape matrix on a species abundance depends to a large extent on the composition and grain size of the landscape in relation to the species life history characteristics (Dunning et al. 1992; Fahrig and Merriam 1994), in particular to its mobility and habitat requirements. For most of the predators we studied, overwintering and breeding occur in different habitats, and individuals must move among habitats during the growing season in order to track ephemeral prey populations. In a diverse, fine-grained landscape, individual predators may not need to travel far to obtain essential resources. In this case the influence of non-cultivated land on the abundance of aphid predators would be relatively local, and species responses to spatial variation in the composition, size, and distribution of landscape elements comprising the matrix would be minimal. In a coarse-grained landscape, matrix effects on local abundance of aphid predators could be accentuated by differences in dispersal characteristics of species which affect their ability to travel the greater distances required to obtain essential resources (Dunning et al. 1992).

We have shown that aphid predators respond differently to variation in the composition and patchiness of the landscape matrix, at least at the characteristic scale of land use in eastern South Dakota. The fact that predator populations in wheat fields are larger when the grain size of the landscape matrix decreases and the amount of non-cultivated land in the matrix increases, suggests that agricultural landscapes in eastern South Dakota are sub-optimal for cereal aphid predators. Thus, it should be possible to enhance populations of cereal aphid predators by manipulating the size, composition, and distribution of landscape elements. From the standpoint of aphid biological control, the optimal landscape would be one which has minimal adverse affects on the predators influenced most by loss of non-cultivated land. In our study those species were *C. maculata* and *H. parenthesis* which, apparently because of their restricted movement compared with other aphid predators, are sensitive to

variation in landscape structure at a relatively fine scale.

We realize that land use decisions rarely center on issues like biological control, and we are not suggesting that they should. However, when alternate choices for land use exist, viable alternatives may sometimes exist that can increase the abundance of natural enemies of crop pests. If implemented, such plans could enhance the prospects for effective biological control and more sustainable crop production. A thorough understanding of the dynamics of predatory insect populations in agricultural landscapes would provide the knowledge needed to evaluate such options.

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## Appendix

*Appendix 1.* Factor loadings for the first seven principal components (L1–L7) based on 15 landscape variables after varimax rotation.

Spatial scale	Landscape variable	Principal component						
		L1	L2	L3	L4	L5	L6	L7
Fine	% grassland & pasture	0.10	0.09	−0.04	0.26	0.90	0.05	−0.02
	% woods	0.03	0.04	0.01	0.14	0.20	0.92	−0.05
	% CRP	0.53	0.02	−0.11	0.15	0.07	0.66	0.07
	% wetlands & water	−0.01	−0.03	0.96	0.07	0.00	−0.07	0.03
	# boundaries crossed	0.12	0.07	0.23	0.19	0.79	0.28	0.05
Intermediate	% grassland & pasture	−0.01	0.29	0.02	0.77	0.30	0.06	−0.04
	% woods	0.51	0.05	−0.07	0.58	0.23	0.36	−0.04
	% CRP	0.88	0.05	−0.00	0.12	0.17	0.01	0.12
	% wetlands & water	0.02	−0.04	0.94	0.01	0.13	0.02	0.15
	# boundaries crossed	0.16	0.17	0.11	0.86	0.15	0.15	0.03
Broad	% grassland & pasture	0.10	0.84	−0.09	0.30	0.11	−0.15	−0.04
	% woods	0.67	0.59	−0.07	0.09	0.00	0.13	−0.14
	% CRP	0.79	0.45	0.13	0.03	0.00	0.18	−0.05
	% wetlands & water	0.03	0.02	0.15	−0.01	0.02	−0.01	0.98
	# boundaries crossed	0.23	0.85	−0.00	0.14	0.07	0.16	0.12